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VI. On Mimicry in certain Butterflies of New Guinea. By F. A. DIXEY, M.A., M.D., F.R.S.

[Read March 6th, 1918.]

IN Seitz's "Macrolepidoptera" (Indo-Australian Region; English Edition, p. 147) under the genus *Huphina*, Fruhstorfer speaks of *abnormis*, Wall., "*euryxanthe*," Honr., and "*ornythion*," Godm. & Salv., as related species. This passage contains two minor inaccuracies and one distinct error. Honrath's insect was named by him *euryxantha*. Oberthür afterwards spelt the name with a final *e*, in which he has been followed by other authors. Standinger, however, in "Iris," and Grose Smith and Kirby in their "Rhopalocera Exotica" rightly give the original spelling. The second inaccuracy is in the name "*ornythion*," which was written by its authors *ornytion*.

These are trivial matters; of greater importance is the statement of affinity between *ornytion* and the other two species. Though it bears so striking a resemblance to *Huphina abnormis*, the relationship of *ornytion* to that butterfly is not close, for it belongs in fact, as shown by structural characters, to the very distinct genus *Delias*. Much confusion has prevailed with regard to all three butterflies now named, and it may be worth while to attempt to clear this up before proceeding to the actual subject of my paper.

In his well-known memoir on the Eastern *Pieridae*, published in 1867, Mr. Wallace described and figured under the name of *Tachyris abnormis* a remarkable Pierine from New Guinea.* He observes that in coloration "it bears a striking general resemblance to the beautiful nymphalideous butterfly, *Mynes Geoffroyi*, which inhabits the same country." The type specimen, which may still be seen in the National Collection, is a female: if Wallace had been acquainted with the male, he could scarcely have avoided noting that it does not possess the anal tuft of hairs which characterises the genus *Tachyris*. But the

* Trans. Ent. Soc. Lond., Series 11I, vol. iv, p. 368; Pl. V11I, fig. 5, \heartsuit

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general appearance of his specimen seemed to him to indicate that it came nearest to such forms as ada, Cram., and claris, Wall., and he therefore placed it tentatively in his genus Tachyris next after those species. In 1889 Messrs. Grose Smith and Kirby * figured both the upper and under side of the same form; Wallace's figure only showing the latter. On the plate in "Rhopalocera Exotica" the species appears under Wallace's name of Tachyris abnormis, but in the text and indices its genus is given as Delias. The figure is said to represent a male, but is really (like Wallace's) that of a female. The mistake as to sex was afterwards corrected by the authors.† In the same work, vol. ii, Pierinae, p. 17, abnormis is once more referred to the genus Delias, and is said to belong to the group of D. ladas, Grose Smith, and D. ornytion, Godm. & Salv. But in the note (Ibid., p. 22) cited above, the authors add, "Herr von Mitis points out ('Iris,' vi, p. 114), that the four-branched subcostal nervure removes both Abnormis and Eurgeantha from Delias." This is quite true; and euryxantha, which appears in the plate (" Rhop. Exot.," vol. ii, Pierinae ; Delias, vi, figs. 7, 8) as a Delias, is in the text called a *Tachuris*.

Honrath,‡ who described *enryrantha* as a variety of *abnormis*, expressed a doubt as to whether Grose Smith and Kirby's figure of *abnormis* represented a male as stated; he adds, however, that those authors in their text rightly placed *abnormis* in the genus *Delias*, "to which genus, instead of to *Tachyris*, Wallace, if he had known the male, would certainly have also assigned it." Staudinger § definitely pronounced Smith and Kirby's figure to be that of a female.

As a matter of fact, neither *abnormis* nor *euryxantha* is either a *Delias* or a *Tachyris*. So far as I am aware, the first author to perceive their true affinity was von Mitis.|| who, as above stated, pointed out that their neuration was not that of *Delias*. Von Mitis himself places them in the neighbourhood of *judith*, *amalia*, *emma*, etc.; *i.e.* in the group named by Moore Huphina, though ranked by the former writer under the wide designation of *Pieris*.

^{* &}quot;Rhopal. Exot.," vol. i, Pierinae, Pl. II, figs. 6, 7.

[†] Ibid. vol. ii, Pierinae, p. 22, note.

Berl. Entom. Zeitschr., xxxvi, p. 435 (1892).

^{§ &}quot;Iris," vii, pp. 117, 118 (1894).

^{||} *Ibid.* vi, pp. 113, 114 (1893),

While there is little doubt that abnormis and euryxantha are best referred to Huphina, it is also true that they appear to stand somewhat apart from other members of that genus. The genitalia of both species are of the Huphina type, but the valves differ slightly in shape from those of *H*, aquata, Gr. Smith, and H. nerissa, Fabr. The genitalia in Delias are quite different. The scent-scales of H. abnormis cannot easily be distinguished from those of *H. curyxantha*. if, indeed, they can be distinguished at all. They are of the Huphina type, though shorter and proportionately broader towards the apex than those of other species of the genus. The difference in neuration between Huphina and Delias is well known. The neuration of abnormis and euryzantha is that of the former genus. Von Mitis agrees with Honrath in attributing Wallace's mistake to the fact that he was only acquainted with the female. Standinger * speaks of von Mitis as having shown that abnormis and euryxantha belong to the genus "Pieris (or Appias)"; but these forms have certainly no more to do with " Appias" than they have with Tachuris, nor did you Mitis suggest the contrary.

As already stated, there is little or no doubt that abnormis and *curyxantha*, whether they are distinct species, or whether, as thought by Honrath, von Mitis and Staudinger, forms of the same species, have their true affinity with the Pierines included in Moore's genus Huphina. This was correctly recognised by Mr. A. G. Butler † in his Revision of that genus. But while rightly placing them in Hupkina, to which group they almost certainly belong, he associates with them in the same genus ladas, ornytion and dohertyi, adding the following comment : "I must confess that the fact of the last five species occurring together in New Guinea, in conjunction with the fact that similarly coloured species of the Nymphalid genus Mynes occur there, is very suspicious. I cannot help thinking that breeding experiments would tend greatly to reduce the number of these 'species' in both genera." Mr. Butler's suspicions that something was wrong were well founded; and it is quite probable that breeding experiments would show that abnormis and euryxantha are conspecific, as was supposed by Honrath, Staudinger and others. But along with

* '' Iris,'' vii, pp. 117, 118 (1894).
† Ann. Mag. Nat. Hist., 7th Series, vol. iii, p. 206 (1899). It may be noted that Mr. Butler's reference to Oberthür's "Etudes" should be to p. 6, not to p. 61.

a possible reduction in the number of species, what is really required in the five forms associated in the "Revision" is an increase in the number of genera. The first two forms of the five, viz. euryxantha and abnormis, belong, as we have seen, to Huphina; but ladas and ornytion are certainly members of the genus Delias. With regard to the fifth species, viz. dohertyi, there is a fresh complication. A Pieris dohertyi from Jobi and a Delias dohertyi from Timor were both described in 1891, the former by M. Oberthiir. the latter by Lord Rothschild. Oberthür's description having been published in August, and Rothschild's in September, it would seem that the former has priority. I have never seen Oberthijr's type, but from the description and figure I have no doubt that it is a Delias. Rothschild's dohertyi is certainly a Delias, and quite distinct from Oberthür's. In his Revision of the genus Delias,* Mr. Butler refers under D. dohertyi to Rothschild's description above mentioned, and also to Grose Smith and Kirby's figures in "Rhopal. Exot.," ii. Delias, Pl. IV (not Pl. VI. as Butler), figs. 7. 8, which represent Rothschild's type. He adds, " It is a curious thing that in the same year when the above was described M. Oberthür described a Pieris Dehertyi from New Guinea. The latter, however, appears to me to be allied to P. ornytion of Godman and Salvin. in which case it is not a Delias (although P. ornytion has erroneously been referred to this genus by von Mitis)." But, as we have seen, ornytion is a Delias, and if Mr. Butler is right, as I believe he is, in thinking that Oberthür's dohertyi is allied to ornytion (of which species it seems to be the representative in the Island of Jobi), we have two dohertyi in the same genus, Oberthür's being apparently the one that is entitled to stand; unless indeed Oberthür's dohertyi should turn out to be a mere synonym of ornytion; in which case I presume that Rothschild's would stand as the true dohertyi. This, however, is a question that I would fain leave in the hands of experts in nomenclature.

Turning now to Fruhstorfer's treatment of these forms, we find that he ends his account of *Huphina* with the same five species as those to which Butler called attention in the passage above quoted, adding to them "*pcrsephone*, Staud, (= *odyssia*, Frust. *i.l.*)." † His notice of this

^{*} Ann. Mag. Nat. Hist., 6th Series, vol. xx, p. 153 (1897).

[†] Seitz, "Macrolepidoptera" (Indo-Australian Region), Engl. Ed., p. 147,

assemblage is no doubt based on the "Revision"; * and we have already seen that three of its members, viz. ornytion, ladas and dohertyi belong not to Huphina but to Delias. There remains persephone, Staud., from Waigiou. This form, as Fruhstorfer says, " was formerly only known in one defective male specimen, and described as Delias." His figure, which appears in loc. cit., Pl. 63 d, as Huphina odyssia, is indistinguishable from specimens of ornytion from the Arfak Mountains in N.W. and from Kapaur in W. New Guinea, on the underside of which forms the submarginal red line of the hind-wing is wanting, and the vellowish patch on the apex of the fore-wing may also be absent, as in the figure of "odyssia." Staudinger + was no doubt right in placing persephone in the genus Delias; there was also some justification for his surmise that a larger number of specimens, perhaps from other localities, might show that persephone is a local form of ornytion. As we have seen, there is no assignable difference between the Waigiou form and specimens of D. ornution from Western New Guinea. Standinger speaks of orngtion as from S.W. New Guinea, but Godman and Salvin's specimens, including the type, were taken near Port Moresby. Even in these the submarginal red line was almost obsolete; in another specimen from Port Moresby it is entirely lacking, as in the type of *persephone*.

We may sum up as follows :----

Abnormis is not a Tachgris (as Wallace, and Grose Smith and Kirby in their plate); nor a Delias (as Grose Smith and Kirby in their text and indices, also Honrath); nor a "Pieris (Appias)" (as Staudinger); but a Huphina (as yon Mitis, 1 Butler and Fruhstorfer).

Euryxantha (not *euryxanthe*) is not a *Delias* (as Honrath in his description and Grose Smith and Kirby in their plate §); nor a *Tachyris* (as the two latter authors in their text and indices); nor a "*Pieris* (*Appias*)" (as Staudinger); but a *Huphina* (as von Mitis, Butler and Fruhstorfer). It may probably be conspecific with *abnormis*.

* The reference to Oberthür's Études, "p. 61" (instead of p. 6), above noted in the "Revision," is repeated in Fruhstorfer's Alphabetical List of Indo-Australian Pierines; *loc. cit.*, p. 185.

† "Iris," vii, p. 355 (1895).

‡ He calls it *Pieris*, but is aware of its true affinities.

§ Both *abnormis* and *euryxantha* are also assigned to *Delias* by Grose Smith in Novit, Zool, i, pp. 334, 335 (1894).

Ornytion (not ornythion), described as a Pieris, is not a Huphina (as Butler and Fruhstorfer); but a Delias (as Staudinger, von Mitis, and Grose Smith and Kirby).

Persephone is not a *Hnphina* (as Fruhstorfer); but a *Delias* (as Staudinger).

Dohertyi, Oberth., described as a *Pieris*, is not a *Huphina* (as Butler and Fruhstorfer); but a *Delias*. The three lastnamed forms are very probably conspecific.

Dohertyi, Roths., is rightly assigned to *Delias* by its describer, by Grose Smith and Kirby, and also by Butler.

Ladas is not a Huphina (as Butler and Fruhstorfer); but a Delias (as Grose Smith and Kirby).

The confusion that has prevailed with regard to these species affords a good illustration of the way in which even skilled entomologists may be misled as to affinity by striking resemblances in colour and pattern. It is surely not unreasonable to suppose that analogous mistakes may be made by insectivorous enemics.

To turn now to the main subject of this paper. It will be observed that all the forms that have been mentioned are inhabitants of New Guinea and adjacent islands; also that, leaving Huphina eurgxantha and the form of Munes geoffroui with a light hind-wing out of account, the remainder are characterised by a uniform dark coloration of the under surface of the hind-wing, in some cases relieved by streaks, touches or lines of bright red. The butterflies in question belong to three different genera; two of the genera, viz. Delias and Huphina, being included in the subfamily *Pierinae*, and the third, viz. *Mynes*, in the subfamily Nymphalinae. Of all these forms, Delias orngtion may perhaps be regarded as the most characteristic. I am not acquainted with the habits and postures of any of the members of this assemblage; but if D, ornytion behaves like most other Pierines, its attitude while feeding or resting during the intervals of flight would show on the underside a striking contrast between the dark hind-wing and apex of fore-wing on the one hand, and the white portion of the fore-wing on the other. The appearance of the butterfly, already conspicuous and distinctive, would be rendered still more so by the red costal streak and red patches or submarginal line of the hind-wing. Huphina abnormis under similar conditions would display the

like contrast between white, blackish brown and searlet, though here it is interesting to observe that on a close comparison the searlet streak in *abnormis* is seen to be not, as in ornytion, on the costa of the hind-wing, but on that of the fore-wing. The thin scarlet submarginal line, often present in ornylion, is also absent from abnormis, though a suggestion of it may occur in the form of a few scarlet patches. Mynes geoffroyi, or rather the form doryca, would present, as was observed by Wallace, the same general appearance as *abnormis*, the contrasting colours being very nearly the same. But here the relative position of the scarlet touches is again somewhat different. Comparing doryca with abnormis, we see a rough correspondence between the scarlet costal streak on the hind-wing of the former and that on the fore-wing of the latter; also between the scarlet submarginal spot on the hind-wing of the latter and that on the fore-wing of the former. As in abnormis, so in doryca, the hind-wing has no scarlet submarginal line. The apex of the fore-wing is in doryca diversified with certain light-coloured marks; these are absent from abnormis, but many specimens of ornytion show a paler area, much less conspicuous than in doryca, but in the corresponding situation.

If these insects, after the usual manner of butterflies, depress the fore-wings during the periods of protracted rest, so as to conceal the white portion of the fore-wing and leave visible only the apex of the fore-wing and the whole expanse of the hind-wing, the resemblance between them becomes perhaps even more detailed. The costal and submarginal red marks fall more nearly into their right relative positions, irrespective of their situation on foreor hind-wing; and the assemblage is now joined by another Delias from New Guinea, viz. D. irma, Fruhst. In the male of this butterfly the under surface of both wings is black, with the exception of a scarlet patch on the costa of the hind-wing, like that of D. ornytion, but somewhat shorter in proportion; there may also be a powdering of orange-vellow scales about the distal end of the cell in the fore-wing, though this is often evanescent or absent.

It is difficult to see how the facts with regard to these four insects can be interpreted without recourse to the theory of mimicry. The resemblance between two of them, as has been seen, has been sufficient to cause great confusion, even on the part of skilled entomologists: and it is hardly necessary to point out the improbability of this striking resemblance between insects differing in affinity, but all inhabiting the same region, being due to simple coincidence. Nor, again, is it easy to suppose any factor in the climate or external conditions of New Guinea which could lead directly, on the part of three or four of its butterflies, to the assumption of a dark underside with red markings; these markings, be it observed, belonging in some cases to the fore-wing, in others to the hind-wing, but always contributing to the same general effect. Whether the explanation founded on mimicry is adequate, can only be finally decided by observation and experiment; at present I think it must be admitted to hold the field.

The scarlet markings on the hind-wing underside of Delias ornution would seem to be an attenuated version of the subcostal red patch and submarginal red band seen in the corresponding position on the hind-wing of Delias harpalyce, Donov., and Delias nigrina, Fabr. This series of markings has a wide distribution among the species of Delias, being more or less completely represented in such species as D. aganippe, Donov. (Australia); D. kummeri, Ribbe, iltis. Ribbe, and bakeri, Kenr. (New Guinea); D. mysis, Fabr. (Australia); D. argenthona, Fabr. (Australia); D. caeneus, Linn. (Moluccas); D. eucharis, Drury (India); D. stolli, Butl. (China); D. eumolpe, Gr. Smith (Borneo). A comparison of these and other forms appears to favour the conclusion that in D. ornytion we have the red submarginal series in an obsolescent rather than in an incipient stage; and it is observable that although the subcostal scarlet patch is persistent throughout the whole range of this species, the submarginal scarlet line, which is nearly always present in specimens from Eastern New Guinea, and is well marked in a specimen from the Louisiade Archipelago, has, in all the examples known to me from Western New Guinea and the adjacent islands, completely vanished without leaving a trace. Now it is to be remarked that the failure of the red line in D. ornution brings its underside, with closed wings, into relation with that of Delias inferna, Butl. (or as Fruhstorfer calls it when it occurs in New Guinea, D. irma). On the mimetic hypothesis, it would be natural to ask whether the darkening of inferna has been influenced by ornytion, and the loss of red in *orngtion* by the condition in *inferna*. No doubt much remains to be discovered about the distribution of these forms in New Guinea, which is a very large country. But as far as is known at present, the disappearance of the red line of *D. orngtion* in the western part of its area cannot be connected with the presence of *D. inferna* or "*irma*," for the latter form appears not to occur in the western half of the island. On the other hand, it would seem to be not impossible that the dark coloration of *inferna* as compared with the other members of the *aruna* group may have been influenced by *orngtion*; for the only region outside the range of the latter where *inferna* occurs appears to be the northern extremity of the Cape York peninsula.

It is doubtful whether any geographical relation can be traced in the case of the red spots of *Huphina abnormis*. The submarginal series of the hind-wing occurs in greater or less development in specimens from Eastern New Guinea, the first at least of the series being apparently always present. The type, which is entirely destitute of the hind-wing series, is said by Wallace to have come from "N.W. Papua"; but the present data are obviously insufficient for forming any conclusion on this head. Nor, again, can it be said that *Mynes doryca*, which is generally distributed throughout New Guinea, shows any difference in the development of its red spots in correspondence with locality.

The facts that can be affirmed with certainty are that these four forms, viz. Delias ornytion, D. irma, Huphina abnormis and Mynes doryca, all resemble each other, and depart from most of their congeners, in the possession of a dark, almost black under-surface to the hind-wing, on which occurs a series of red markings in a greater or less state of development; that in two of them (Mynes and Huphina) the red series is divided between fore- and hind-wing, but presents the same general appearance as in the two *Delias* in which it is to be seen on the hind-wing alone; and that in one of the four (D. irma) the under-surface of the foreas well as of the hind-wing is dark, so that in the other three the attitude of complete rest (fore-wings depressed between hind-wings) must be adopted in order to produce resemblance to the first. Whether these facts are open to an interpretation on the basis of the theory of mimicry is a question which will be answered in different senses by different authorities; but to those who admit the

validity of the theory in any form, it will seem probable that some mimetic influence at any rate has here been at work, though it may not be possible to determine its exact extent.

We have seen that there is little doubt that the markings on the hind-wing underside of D. aganippe are generally homologous with those in the corresponding situation of D. niaripa; and equally little doubt that the searlet markings of D. ornution are an attenuated version of the subcostal patch and red band or chain of spots seen in the two former and many other species of Delias, especially those belonging to what may be called the eucharis section of that genus. In Trans. Ent. Soc. Lond., 1891, pp. 300, 301, and Proc. Ent. Soc. Lond., 1909, p. exiii, reasons were given, on the combined evidence of wing-markings and scent-scales, for supposing that the *euchuris* section is a natural group distinct from the belisama section, though no doubt at one time linked with it through a form more or less resembling Delias aganippe. D. inferna, which is a local race of D. aruna, Boisd., is shown by both kinds of evidence to be closely akin to belisama, and so to belong to an assemblage in which the red subcostal patch is nearly always present, and the red submarginal chain is as a rule not to be found.* It was therefore rather to be expected, on the theory of a mutual approach between D. inferna and D. ornytion, that the latter should be more apt to lose the already attenuated submarginal line than the former to revive it or start it afresh.

Two other points of interest in connection with this assemblage remain to be noticed.

(1) With regard to $Mynes \ doryca$ it is to be remarked that not only does the underside recall in a striking manner the appearance of *Delias ornytion* and *Huphina abnormis*, but its upperside also is of a Pierine rather than of a Nymphaline character. On a superficial view there is little to distinguish it from the female of *D. ornytion* or of *H. abnormis*, and the same applies to the probably conspecific form, *M. gcoffrogi*. The facies is the not unusual Pierine arrangement of a pale area surrounded by a dark border, broader in the Pierine female than in the male.

^{*} It is, so far as I am aware, only present among *Delias* of the *belisama* group in *D. eumolpe*, Gr. Smith, from North Borneo and *D. funerea*, Roths., from Hahmaheira.

It is further remarkable that the same aspect is shared on the upperside by the male of Nepheronia (Pareronia of Bingham) jobaca, Boisd., the representative of its genus in Ceram, Bouru, Western New Guinea and the adjacent islands. It is well known that the females of Nepheronia are minics of other butterflies, chiefly Danaines and Papilionines, that inhabit the same regions. The males. however, are not usually considered to be mimetic, with the exception perhaps of N. tritaea, Feld., of Celebes, N. argolis, Feld., of the Moluccas, and N. phoeaea, Feld., of the Philippines. But the contrast between the uniformlytinted ground-colour of N. jobaea \mathcal{Z} and the black veining of the upper surface of the male Nepheronias from further west, such as N. hippia, Fabr., and pingasa, Moore (mainland), naraka, Moore (Andamans), valeria, Cram, (Java and Sumatra), boeberg, Eschsch. (Philippines), is so striking as to suggest the possibility that this Nepheronia has been influenced in a mimetic direction by the New Guinea assemblage now under discussion. As between the Nepheronia and the Munes, the correspondence is specially close, for it extends even to the tint of the pale area of the wing, which in neither butterfly is pure white. In both species the disc of the hind-wing is pale greyish blue; and that of the fore-wing is pale greenish yellow in the Mynes, and either that or very pale blue in the Nepheronia. It may also be remarked that the underside of N. jobaea \mathcal{Z} , by its dark hind-wing, does to some extent recall the underside of M. doryca, D. ornytion and H. abnormis, though it is entirely devoid of red spots or streaks. This feature of the hind-wing is exceptional in Nepheronia, though some approach to it is visible in N. argolis. A somewhat similar underside to that of N. jobaea \mathcal{F} is seen in Delias ladas, Gr. Smith, the range, however, of the latter insect appears to lie outside of the region inhabited by N. jobaea.

(2) It was mentioned above that Huphina abnormis and H. euryxantha are believed by some good authorities to be conspecific. Whether this be so or not, there is no doubt that the two forms are at least very closely allied. Each possesses an underside which presents a type of coloration very different from that which is usual in the genus; and it is interesting to remark that while H. abnormis bears a strong resemblance to one Delias, viz. D. ornytion, the very different underside of H. curyxantha at once recalls the Delias forms of the mysis group, particularly D. lara,

Boisd., which, like *euryxantha* itself, is an inhabitant of New Guinea.

It is obvious that with regard to all these forms much remains to be learned concerning their relative frequency, their exact distribution and local variation, their modes of flight and postures during rest, and the extent to which they are the prey of insectivorous birds or other enemies. Only when more data are forthcoming on these heads will it be possible to pronounce with any approach to confidence on their respective bionomic relations.

My thanks are due to Lord Rothschild, F.R.S., for personal help in examining the collections at Tring; and to Dr. Eltringham for his skilful preparations of the genitalia mentioned on p. 120.

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